ments could be made. Those which were chosen as fundamental are:

$m \wedge m$, $110 \wedge \bar{1}10 = 90° \, 12'$ $m \wedge p$, $110 \wedge 221 = 24° \, 37'$ $a \wedge p$, $100 \wedge 221 = 49° \, 53'$

The axial ratio and forms are as follows:

$$\grave{a} : \bar{b} : \dot{c} = 0{\cdot}9965 : 1 : 0{\cdot}7698 \qquad \beta = 100 \wedge 001 = 89° \, 53\tfrac{1}{2}'$$

a, 100, i-$\bar{i}$	m, 110, I	d, 403, $-\frac{4}{3}$-$\bar{i}$	s, $\bar{4}03$, $\frac{4}{3}$-$\bar{i}$	p, 221, —2
c, 001, 0	n, 130, i-$\grave{3}$	e, 203, $-\frac{2}{3}$-$\bar{i}$	u, $\bar{2}03$, $\frac{2}{3}$-$\bar{i}$	o, 263, -2-$\grave{3}$

The pyramids *p* and *o* were frequently wanting. The orthodomes *d*, *e*, *s* and *u* were very constant in their development and gave to the crystals an orthorhombic habit. Owing to the curved and striated character of the faces the symmetry could not be satisfactorily determined by measurement, but the optical properties showed that the crystals were truly monoclinic. In polarized light the tables show an extinction parallel to the ortho- axis and in convergent light one of the optical axes and the acute bisectrix can be seen near the limits of the field. The plane of the optical axes is the clinopinacoid.

These two salts, although entirely different in crystalline habit, are very similar in their axial ratios.

Sheffield Scientific School,
April, 1892.

ART. XIX.—*Development of the Brachiopoda.* Part II. Classification of the Stages of Growth and Decline; by CHARLES E. BEECHER. (With Plate I.)

A BRIEF review of the known embryology of the Brachiopoda is desirable, in order to account for some of the differences presented by adult forms in the several divisions of the class. This knowledge is far from complete, and is confined to a few species, but much of interest bearing on the later development of the organism may be obtained.

The important memoirs of Morse,*[18, 19] Kovalevski,[15] Lacaze-Duthiers,[16] and Shipley,[22] contain nearly all that is known regarding the early embryology of brachiopods. The genera included in the works of these authors comprise Cistella, Terebratulina, Liothyrina, and Lacazella. Later larval stages of the genus Glottidia have been fully described by Brooks.[4] Müller,[20] also, has given a description and figures of a larval form doubtfully referred to Discinisca. The results of these observers must at present be taken without reservation, and are thus made use of in the present paper.

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* The works referred to by numbers are cited in full in the list appended to this article.

Something is known, therefore, of the early stages in each of the four groups or orders proposed by the writer.[1] The Atremata, Neotremata, and Protremata are represented by a single genus only in each; Glottidia, Discinisca, and Lacazella, respectively; and the Telotremata, by Cistella, Terebratulina, and Liothyrina. Were Glottidia and Discinisca as well known as Cistella, Terebratulina, and Lacazella, some comparisons could undoubtedly be made which would enlighten many obscure points of anatomy and morphology, as well as give clearer insight into the history and origin of each group.

Cistella and Terebratulina are taken as standards of the embryological development on account of the completeness with which they have been studied, and because their points of difference are not great. Lacazella shows such peculiar features, that its history must be discussed separately. The nepionic Glottidia and Discinisca, too, present characters which evidently had an early history somewhat different from Cistella or Terebratulina.

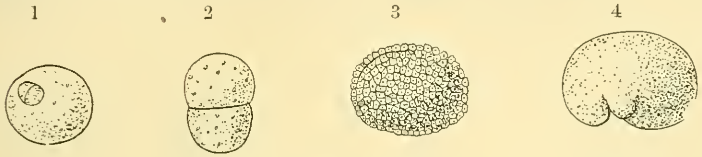
In taking up the review of the observed stages of growth, an attempt will be made to fix their limitations. To this end the admirable nomenclature proposed by Hyatt[9, 10] is here adopted, as it is more convenient and of wider application and significance than the terms heretofore used. Thus far this system has been employed principally in studies relating to the mollusca, and its application to the Brachiopoda will necessarily require some illustration and explanation. In the preface to "Genesis of the Arietidæ," Hyatt has presented a summary of the theoretical opinions resulting mainly from his studies in the Cephalopoda. It is believed that nearly the same ground may be covered in the Brachiopoda, and thus the truth of these deductions will receive further evidence from another class of organisms.

Embryonic stages.

The true embryonic stages are classified by Hyatt as *Protembryo*, *Mesembryo*, *Metembryo*, *Neoembryo*, and *Typembryo*. To these Jackson[11] has added the *Phylembryo*, taking it from the later stages of the Typembryo to represent the period when the animal can be referred definitely to the class to which it belongs.

The succeeding stages in the growth of the animal to maturity are termed by Hyatt *nepionic* (young), *nealogic* (adolescent), and *ephebolic* (mature), while old age characters are called *geratologic*. The subject of geratology is further divided into the *clinologic* and *nostologic* stages.

The application of this nomenclature of the stages of growth and decline to the Brachiopoda is shown on the following pages.



Cistella neapolitana Scacchi.

FIGURE 1.—Protembryo. Unsegmented ovum.
FIGURE 2.—Protembryo. Ovum composed of two spheres.
FIGURE 3.—Mesembryo. Blastosphere.
FIGURE 4.—Metembryo. Gastrula. (1-4, after Shipley.)

The *Protembryo*, as in other groups of organisms, includes the ovum and its segmented stages preceding the formation of a blastula cavity. Figures 1, 2, show protembryonic stages of Cistella. The eggs are spherical, pyriform or ovoid, and the segmentation proceeds in a regular manner, resulting in a blastosphere composed of equal parts.

The *Mesembryo*, or blastosphere, figure 3, has been observed in Cistella, Terebratulina, and Lacazella. The blastula cavity is small.

The *Metembryo*, or gastrula stage, figure 4, is developed from the blastosphere in two ways; (*a*) by embolic invagination in Cistella and Terebratulina (Kovalevski and Shipley), and (*b*) by delamination in Lacazella (Kovalevski). At the close of this stage, the archenteron in Cistella is trilobed, consisting of a central cavity, or mesenteron, connecting on each side with the body cavity.

The *Neoembryo*, represented by the trochosphere and segmented ciliated cephalula stages, has been more fully observed than any of the preceding. The first advance from the completed gastrula is in the separation of the mesenteron from the body cavity, and the division of the organism into two segments or lobes, the cephalic and caudal, figure 5. Later a third or thoracic segment is developed and carries four bundles of stiff barbed setæ, figure 6. The cephalic and caudal lobes are densely ciliated. During the subsequent cephalula period, two eyes, then two others appear in Cistella, and at the same time the dorsal and ventral sides of the thoracic segment become extended over the caudal, and are progressively defined as two lobes, figures 5–9, 24, 25.

Terebratulina has a tuft of bristles on the top of the cephalic segment. In Lacazella, the bundles of setæ are absent, and the head is more distinctly differentiated from the anterior segment than in Cistella. The closing cephalula stage in Cistella has an umbrella-like expansion of the cephalic border, and the organism becomes a free swimming larva, figures 7–9.

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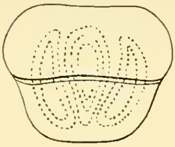

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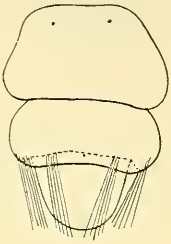

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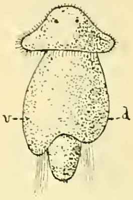

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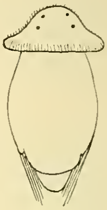

Cistella neapolitana Scacchi.

FIGURE 5.—Neoembryo. Embryo of two segments.
FIGURE 6.—Neoembryo. Cephalula, ventral side; showing cephalic, thoracic, and caudal segments, eye spots, and bundles of setæ. (5, 6, after Kovalevski.)
FIGURE 7.—Neoembryo. Lateral view of completed cephalula stage; showing extent of dorsal (*d*) and ventral (*v*) mantle lobes, and umbrella-like cephalic segment.
FIGURE 8.—Neoembryo. Same stage; ventral view. (7, 8, after Shipley.)

Larval stages.

The *Typembryo* is the larval stage at which some distinctive features make their appearance, but before the special characters of the class are to be found, figure 10. It is analogous to the molluscan embryo in which a shell gland and plate-like initial shell are developed. There is, however, no homology of parts or organs between the typembryonic mollusk and brachiopod.

In Cistella and Terebratulina the development of the typembryo has been observed, and consists of the folding upwards of the lobes which have been developed from the thoracic segment to form the mantle, so that they gradually enclose the anterior end, figures 24–27. The surfaces of the mantle which were exterior in the cephalula have now become inner and the bundles of setæ have revolved 180°, changing their direction from posterior to anterior. This leaves the lower part of the thoracic and the whole of the caudal segment exposed. The outer surface of the mantle is invested with a hard integument, which, upon completion, and before the growth of the true shell forms the protegulum. The pedicle at this stage is also defined, being a modification of the caudal segment. It may serve to attach the larva to foreign objects, as in Cistella, figure 10, and Terebratulina, or it may remain undeveloped for a time as in Glottidia and Discinisca. A rudimentary digestive tract is present.

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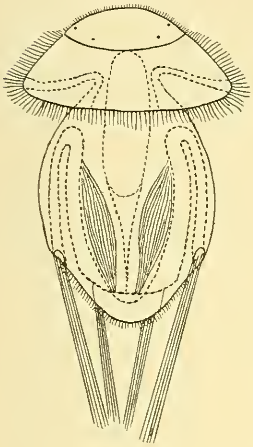

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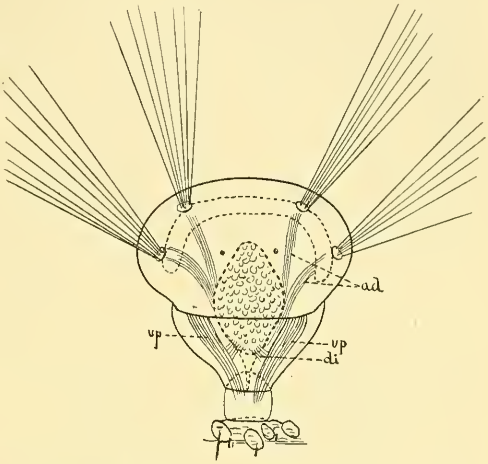


Cistella neapolitana Scacchi.

FIGURE 9.—Neoembryo. Completed cephalula stage.

FIGURE 10.—Typembryo. Transformed larva resulting from folding upwards of mantle lobes over cephalic segment: *ad*, muscles from bundles of setæ to sides of body cavity; *di*, muscles from dorsal to ventral sides of body; *vp*, muscles from ventral side of body to caudal segment or pedicle. (9, 10, after Kovalevski.)

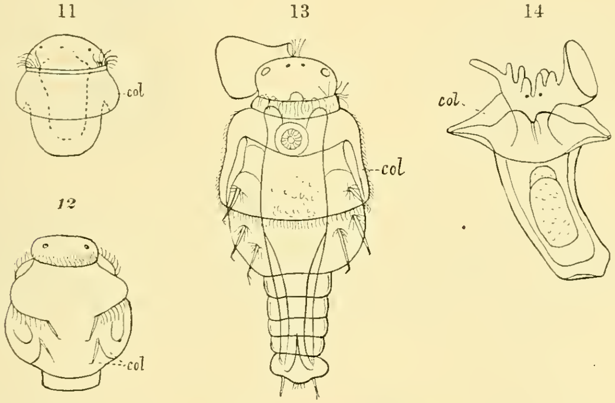
The body muscles which have been developed thus far consist of four distinct pairs. Two pairs lie close to the sides of the body cavity, and extend to the points of insertion of the bundles of bristles, figure 10, *ad*. They become after transformation the four adductor muscles of the valves. The third pair extends from the ventral side of the body to the caudal segment, and is converted into the ventral pedicle muscles, figures 10, 15, 16, *vp*. The fourth pair is situated posterior to the digestive tract, and extends from the dorsal to the ventral wall of the body, figure 10, *di*. They form the divaricator muscles in the mature brachiopod, figure 16, *di*, and are divided into or duplicated by a pair of dorsal and a pair of ventral divaricators. There is also a pair of dorsal pedicle muscles in the larva of Liothyrina and Terebratulina.

The folding upwards of the mantle lobes forms the first hinge line of the future valves, *hl*, figures 26, 27. Thus its origin is not, as in pelecypods, a line produced by the bending of a single plate (Jackson), but is the line along which the two mantle lobes are bent against the body. Between them projects posteriorly nearly half the body of the animal, and the whole opening corresponds to the pedicle opening of later stages of growth. The hinge of brachiopods, therefore, is not primarily a line of articulation of the valves, but the limiting borders between the body and the attached edges of the mantle. Secondarily, and during later growth, the extension of the valves along a line of apposition forms a true hinge line.

The first points of contact of the valves to form the true hinge lie adjacent to the right and left sides of the body of the animal, at the cardinal extremities, figure 15, *t*. Here naturally the first hinge teeth are formed, and their position corresponds to that in adult individuals; namely, on each side of the cardinal opening. The enlarging of the cardinal opening by shell growth results in the gradual divergence or separation of the teeth as in Terebratulina. In species with extended hinge lines, as in many forms of Spirifer, Orthis, and Strophomena, the teeth still lie in their original position on each side of the cardinal opening, and the elongation of the hinge has come not only from the enlargement of the opening by growth, but by additions at the hinge extremities, so that the teeth are situated on each side of the central area, below the beak, and not at the cardinal angles. The young of these genera, however, all have the hinge teeth at the extremities of the hinge, as the cardinal opening then occupies the whole posterior area of the shell.

Adult specimens of Kutorgina (*K. cingulata* Billings) have a deltidium as in Strophomena. The cardinal opening including the deltidium occupies the whole posterior end of the shell, and according to a statement made to the writer by Mr. Charles Schuchert, there are rudimentary teeth at the cardinal extremities. Therefore, this genus represents a nepionic condition of later forms, and, on account of these and other characters, it is believed to be related to Orthisina and Strophomena, of which it is the ancestral type. It consequently belongs to the articulate brachiopods.

The embryonic stages up to this point have frequently been compared to similar stages in other organisms, especially in the Annelida and Polyzoa. Without repeating these comparisons, which may be consulted elsewhere, [4, 12, 15, 16-19, 21] attention is called to the similarity of development of the brachiopod typembryo to the larval stages of Spirorbis. There are, however, important structural differences. An article by J. W. Fewkes, "On the Larval Forms of *Spirorbis borealis* Daudin,"[7] contains a nearly complete and very interesting account of the development of this chætopod. There is a striking resemblance in the characters of the cephalula stages in both organisms, as may be seen on comparison, figures 11, 12. Spirorbis develops a posteriorly directed extension from the middle segment, called a collar, which in later stages is reflexed anteriorly so as to cover more or less the cephalic portion, thus agreeing with the growth and change in position of the mantle in Cistella. The ventral lobe is also the larger in both. Many other comparisons and homologies have been made by Morse,[19] and the one here described is even more marked than his reference to the lobation of the cephalic collar in Sabella. Four figures are introduced illustrating the principal changes in Spirorbis. They may be compared with the development of Cistella shown in figures 6–10.



Spirorbis borealis Daudin.

FIGURE 11.—Cephalula, developing lobe from the body (*col.*).
FIGURE 12.—More advanced stage.
FIGURE 13.—Larval form before transformation; showing posteriorly directed expansion (*col*) from thoracic segment.
FIGURE 14.—Transformed Spirorbis; showing folding upwards of collar partially enclosing head. (11–14, after Fewkes.)

It is not intended by this to indicate a close relationship with the chætopods, for the writer is inclined to accept the opinion of Joubin,[12] that the brachiopods constitute a distinct and independent class.

The *Phylembryo*, figure 15, differs from the Typembryo in (*a*) the completion of the embryonic shell, or protegulum; (*b*) the first appearance of the tentacular lobes of the lophophore, or arms; (*c*) the usual dehiscence of the four bundles of setæ; (*d*) the obsolescence of the eyes; (*e*) the definition of the œsophagus and stomach; and (*f*) the agreement of the muscular system with that in adult forms. These features, with the pedicle which appeared in a preceding stage, represent the brachiopod phylum, and are properly referred to the phylembryonic period of Jackson. Although the molluscan stage called the prodissoconch in pelecypods, the protoconch in cephalopods and gastropods, and the periconch in scaphopods, represents the completed phylembryo of these groups, as the protegulum represents a like period in the developing brachiopod, yet there is no homology of distinctive organs.

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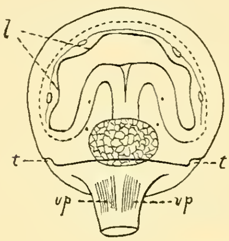

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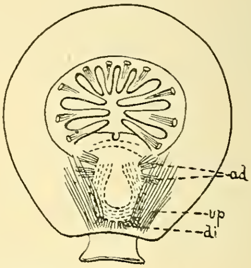

Cistella neapolitana Scacchi.

FIGURE 15.—Phylembryo. Brachiopod; showing shell (protegulum), beginning of tentacles of lophophore (*l*), obsolescence of eye spots, and formation of œsophagus. *t*, hinge teeth; *vp*, ventral pedicle muscles

FIGURE 16.—Nepionic brachiopod; showing distinct tentacles of lophophore, mouth and stomach, and transformation of muscles from typembryo, figure 10; *ad*, adductors; *di*, divaricators; *vp*, ventral pedicle muscles. (15, 16, after Kovalevski.)

The mantle of mollusks is first formed on the posterior dorsal side, and is in the shape of a disc, which gradually envelops the animal to a greater or less extent, and may become distinctly lobed. As has been shown, this organ in the brachiopods develops simultaneously from the dorsal and ventral side of the thoracic segment of the cephalula, and is primarily bilobed.

The initial shell of brachiopods is not produced from a distinct shell gland, as in the mollusca, but is an integument of the surface of the mantle lobes, and intimately connected with them. The position of the valves is dorsal and ventral. The pedicle has no organic similarity with either a foot or a byssus.

The mouth of mollusks (and annelids) is formed below the base of the cephalic lobe of the cephalula, and may be the blastopore, while in the brachiopods it is near the anterior pole within the cephalic segment. Notwithstanding these differences, so many parts are functional equivalents, that their growth and development may be discussed and interpreted in the same terms.

Before passing to later stages of growth which become more and more divergent from a common simple type, some points previously omitted, relating to Thecidium (Lacazella), Lingula (Glottidia), and Discinisca, should be here noted. As Lacazella is a form in which the ventral valve in the nealogic and ephebolic stages is cemented to foreign objects by calcareous fixation, it bears about the same relation to other brachiopods that Ostrea bears to Avicula, among the pelecypods, and a corresponding early absence, or modification, of many features present in adult individuals should be looked for. From what is known of the geological history of Thecidium, and if the interpretations of its phylogeny by the writer are correct, it is derived from an ancestry which had a similar condition of fixation as early as the Upper Silurian. Thecidium is apparently not a terebratuloid genus. Its structural affinities are evidently with the strophomenoids, especially such forms as Plectambonites, Leptænisca, etc. Briefly the reasons for this statement are (*a*) the presence of a deltidium of one plate; (*b*) the absence of a true loop supporting the arms (the internal calcification or spiculization is confined wholly to the mantle, and does not extend to the arms[16]); (*c*) a concave place in the cavity of the ventral beak, bearing the divaricator muscles; (*d*) the attached ventral valve, and (*e*) the cardinal processes in the dorsal valve.* The first character is of prime importance, because all the strophomenoids and none of the terebratuloids have a deltidium of one plate.

It would appear, therefore, that the early, free swimming, larval state, and the later pediculate stage have become lost by acceleration, thus accounting for the very unequal development of the mantle lobes in the cephalula stage, and the non-active and early sedentary larvæ as described by Kovalevski and Lacaze-Duthiers.

The young Lingula (Glottidia) described by Brooks,[4] and the Discinisca by Müller,[20] both representing the phylembryonic stage, were active and free swimming animals, with rudimentary pedicles. Terebratulina becomes attached or rests on the caudal segment during the cephalula stage (Morse), while at the end of this period in Cistella (Kovalevski and Shipley), there is an active, swimming, ciliated organism, which later attaches itself by the pedicle in the typembryonic period.

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* Dall in 1870 (Am. Jour. Conchology) made a clear statement of the characters of Thecidium and of many of its radical points of difference with the Terebratulidæ, showing that it was entitled to rank as the type of a distinct family.

From the facts, that young individuals of paleozoic species belonging to such genera as Zygospira, Spirifer, Orthis, Rhynchonella, and Scenidium, have been observed by the writer to retain their original relations to the objects of support, and that casts of the pedicles of fossil Lingulæ and Eichwaldia have been described (Davidson,[5] Walcott[23]), it cannot be assumed that the free swimming condition was ever present in nealogic or ephebolic individuals. Evidently it has always been a larval character.

Origin of the deltidium and deltidial plates.

The origin and significance of the deltidium* (="pseudo-deltidium") are made apparent in the development of Thecidium, and it may be well in this place to make a few observations on the genesis of this important character, and its relations to the deltidial plates of other genera, as Rhynchonella and Terebratula. It has been already noted (Part I), that the deltidium in all species possessing it (the Protremata) is an embryological, or nepionic feature, which may or may not continue to the ephebolic period; while the deltidial plates in other brachiopods (the Telotremata) appear later during the nealogic and ephebolic periods, or may never be developed. The detailed researches of Kovalevski on Cistella and Thecidium, together with other observations now first made, furnish data for a clear understanding of these differences.†

Figure 18 represents a dorso-ventral section of a ripe cephalula just before the transformation, and shows the unequal lobes of the mantle, *v* being the ventral lobe, and *d* the dorsal; *h* is the head, and *p* the caudal segment developing into a pedicle. A deposit of integument representing the shell has formed on the inner side of the dorsal mantle lobe (*ds*), and also on the adjacent dorsal side of the body lobe (*del*). A larva somewhat more advanced is represented in figure 17, as viewed from the dorsal side. The mantle lobe is still directed posteriorly, as in the preceding figure, and the underlying shell plate is shown

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*The single plate or covering to the triangular opening beneath the ventral beak should be termed the *deltidium*, as it was thus extensively used by Davidson. When it consists of two plates they may be called *deltidial plates*. These names have been loosely used. In Part I of this paper the deltidium proper is referred to as pedicle covering, pedicle sheath, and pseudo-deltidium. Hall and Clarke have proposed to call the triangular opening in the beaks of brachiopods, the *delthyrium*, and the concave plate in the ventral beak of Pentamerus, Orthisina, etc, they have termed the *spondylium*. There yet remains a term for the convex plate covering the opening below the beak of the dorsal valve, and resembling the deltidium of the opposite valve. For this feature the name *chilidium* (*χειλος*) is here proposed.

† Kovalevski.[15] For Thecidium consult the explanation of Pl. IV, figs. 15–26. For Cistella, Pl. I, figs. 13–15; Pl. II, figs. 17, 19–21.

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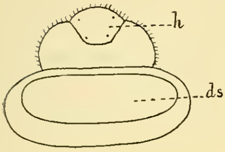

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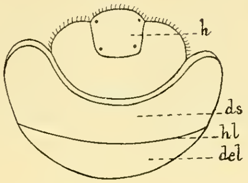

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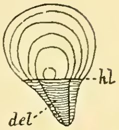

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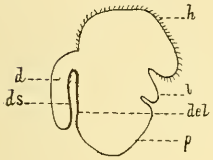

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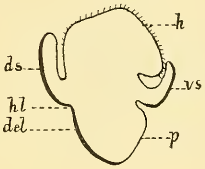

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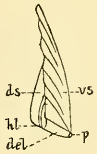

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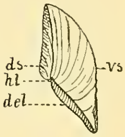

Thecidium (*Lacazella*) *mediterraneum* Risso.

FIGURE 17.—Cephalula; dorsal side. *ds*, dorsal shell plate; *h*, head. (After Kovalevski.)

FIGURE 18.—Dorso-ventral longitudinal section of cephalula of about same age as preceding. *h*, head; *d*, dorsal mantle lobe; *v*, ventral mantle lobe; *ds*, beginning of dorsal valve; *del*, shell plate forming on dorsal side of body; *p*, pedicle. (After Kovalevski.)

FIGURE 19.—Typembryo. Larva transformed from folding upwards of mantle lobes. *h*, head; *ds*, dorsal valve; *hl*, hinge line of dorsal valve; *del*, shell plate on body and pedicle posterior to hinge line of dorsal valve. (After Kovalevski)

FIGURE 20.—Dorso-ventral longitudinal section of preceding. References as in figure 19. *vs*, ventral valve.

FIGURE 21.—Profile view of nealogic *Leptæna rhomboidalis*. The features of the shell are placed and lettered as in figure 20. *ds*, dorsal valve; *hl*, hinge line; *del*, deltidium; *p*, pedicle opening; *vs*, ventral valve.

FIGURE 22.—Adult *Thecidium* (*Lacazella*) *mediterraneum*; dorsal side; showing ventral area and deltidium.

FIGURE 23.—Profile of same. References as in figures 20 and 21.

at *ds*. In the process of transformation (figs. 19, 20), the mantle lobe is turned forwards in the usual manner, bringing the shell on the outside of the animal, so that both dorsal plates are now exposed, *ds* being the dorsal valve, and *del* the shell developed on the dorsal side of the walls of the body and caudal segments. As this plate (*del*) is below or posterior to the hinge line (*hl*), and extends down over the pedicle, it is evidently the beginning of the deltidium. At the same time, there is an extension of the edges of the mantle and pedicle on the ventral, or lower side, and shelly matter is deposited, forming the ventral valve (*vs*), figure 20. At this stage the hinge line, figures 19, 20, *hl*, is the line between the dorsal mantle shell (*ds*) and the dorsal body shell plate (*del*). The beak of the ventral valve is separated from the dorsal beak by the pedicle and the shell covering to the pedicle and body lobe, or the deltidium. The valves afterwards meet at their peripheries, the hinge is extended beyond the deltidium, forming the true hinge of articulate brachiopods. As there is no motion between the ventral valve and deltidium, the two become ankylosed. Figures 22, 23, showing an adult Thecidium, are lettered in the same manner as the preceding, and express the same relation of parts.

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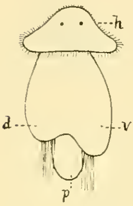

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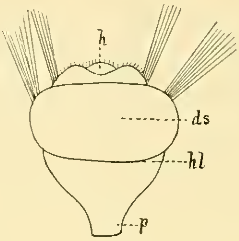

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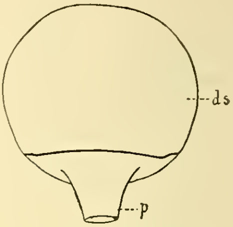

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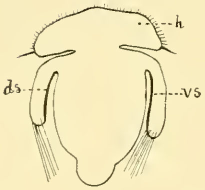

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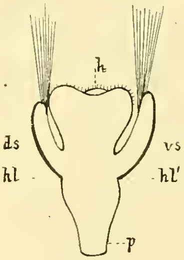

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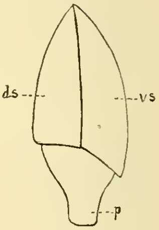

Cistella neapolitana Scacchi.

FIGURE 24.—Lateral view of completed cephalula stage. *d*, dorsal lobe of mantle; *v*, ventral lobe. (After Shipley.)

FIGURE 25.—Dorso-ventral longitudinal section of same: showing posteriorly extended mantle lobes. *ds* and *vs*, inner surfaces of mantle lobes which are to form dorsal and ventral valves. (After Shipley.)

FIGURE 26.—Typembryo. Dorsal view of larva after transformation. *h*, head; *ds*, dorsal valve; *hl*, hinge line of dorsal valve; *p*, pedicle. (After Kovalevski.)

FIGURE 27.—Dorso-ventral longitudinal section based on preceding; showing mantle lobes directed forwards, bringing interior shell-secreting surfaces, *ds* and *vs* of figure 25, on the exterior. *h*, head; *ds*, dorsal valve; *hl*, dorsal hinge; *vs*, ventral valve; *hl′*, ventral hinge; *p*, pedicle.

FIGURE 28.—Dorsal view of early nepionic shell, showing large posterior opening between valves. (After Kovalevski.)

FIGURE 29.—Profile of same. *ds*, dorsal valve; *vs*, ventral valve; *p*, pedicle.

The deltidium is not, therefore, primarily, on account of its manner of origin, an integrant part of the ventral valve, but is a shell growth from the dorsal side of the body, which afterwards becomes attached to the ventral valve, and is then considered as belonging to it.

The further growth of the deltidium around the body and pedicle, and its consequent extension into the cavity of the ventral umbo, may explain the origin of the spondylium.

Kovalevski[15] believed the ventral valve in Thecidium was secreted by the expanded edges of the pedicle and the body walls, whether or not this is so does not affect the interpretation of the origin of the deltidium. From the observations of Lacaze-Duthiers,[16] it seems, however, as though the ventral mantle lobe must have formed the shell in the usual way. This appears all the more probable from the fact, that the lower or ventral valve is punctate, and, so far as known, the mantle contains all the cæcal prolongations, which alone could produce the punctate structure. Careful microscopic examination has failed to detect punctæ in the deltidia of Thecidium, Strophomena, Leptæna, and other punctate genera belonging to the Protremata.

It is true that Aulosteges has spines on the deltidium, but spines even when tubular are not equivalent to punctæ, as shown in Productus, Strophalosia, and some species of Spirifer. Aulosteges is a geratalogous genus, which has become excessively spinose, and has also reverted to ancestral characters in its high hinge area and conspicuous deltidium. It is well known that even the spires of Spiriferina and the loop of Macandrevia are spinose.

Turning now to Cistella as a representative of the Telotremata, a different process obtains.

Figure 24 represents the fully developed, free swimming cephalula of Cistella, and shows the extent of the folds of the mantle and their posterior direction. Figure 25 represents the same in section. The inner sides of the mantle lobes are to form the future valves, the dorsal *ds*, and the ventral *vs*. The transformed larva or typembryo is represented in figure 26 and in section in figure 27. It is seen that the transformation consists in the folding forwards of the mantle lobes over the head segment *h*. Now the shell-secreting layers of the mantle are exterior, and the two valves begin to form, the dorsal shell *ds*, and the ventral *vs*. The pedicle and posterior portion of the body come out freely between the valves and mantle lobes and limit the hinge areas of both, *hl* anp *hl'*.

The further process of growth increases the distance between the initial dorsal and ventral hinges, for while the original dorsal beak is usually maintained at the hinge line, the ventral beak is progressively removed and the ventral hinge travels from its first position at the beak, along the edges of the umbo leaving an open triangular area or delthyrium in the ventral valve occupied by the pedicle. This condition represents the extent of the development of these parts in *Meristina rectirostra* Hall or *Gwynia capsula* Jeffreys, which lack deltidial plates in the adult shell. The young of other telotremate species, as *Magellania flavescens* or *Terebratulina septentrionalis*, agree in the same respect.

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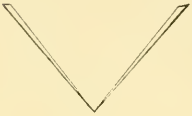

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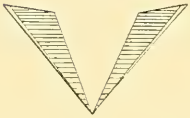

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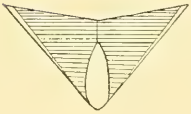

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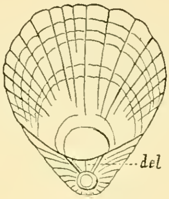

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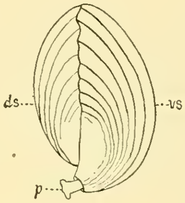

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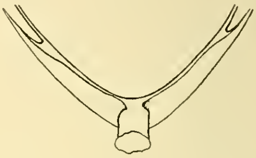

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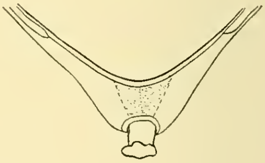

FIGURE 30.—Delthyrium of young Rhynchonella, without deltidial plates.
FIGURE 31.—The same at a later stage, with two triangular deltidial plates.
FIGURE 32.—The same after completed growth; showing joining of deltidial plates, and limitation of pedicle opening to ventral beak.
FIGURE 33.—Dorsal view of *Magellania flavescens;* showing completed deltidial plates, *del.*
FIGURE 34.—The same; profile. *ds*, dorsal valve; *vs*, ventral valve; *p*, pedicle.
FIGURE 35.—Dorsal view of umbonal portion of adult *Terebratulina septentrionalis*, with shell removed by acid; showing slight secondary extension of ventral mantle around pedicle (consequently small deltidial plates are secreted in this species). Mantle areas secreting deltidial plates are shaded.
FIGURE 36.—Dorsal view of umbonal portion of *Magellania flavescens*, with the shell removed by acid; showing the complete envelopment of base of pedicle by secondary expansions from ventral mantle, and consequent production of deltidial plates filling delthyrium except at pedicle opening. See figure 33.

An examination of the animal at this stage shows that the mantle lobes line only the interior of the valves proper. The exposed edges of the mantle are around the peripheries of the valves and also that portion of the ventral mantle border limiting the deltidial opening and passing along the sides of the pedicle at its base. The ventral mantle gradually extends from each side as two prolongations partially covering the opening and enveloping the proximal portion of the pedicle.

As this is an extension of the shell-secreting surface of the mantle, there naturally results the formation of two plates within the deltidial area. Their structure is commonly punctate whenever the valves are punctate.

These outgrowths or extensions of the mantle into the deltidial area finally touch and coalesce until, as in *M. flavescens*, the pedicle emerges through an opening in the ventral mantle, and *pari passu* the deltidial plates unite and limit the pedicle opening to the beak of the ventral valve. The latter process has been carefully described by Deslongchamps,[6] Clarke and the writer[3] and need not be dwelt on here. Figures 35 and 36 of the beaks of *T. septentrionalis* and *M. flavescens* with the shell removed show the relations of the ventral mantle to the pedicle, and the portions which secrete the deltidial plates.

The deltidium and delthyrium are often simulated in the growth of the *dorsal* valve in genera having a high cardinal area in this valve. Orthis, Leptæna, Clitambonites, Spirifer, and Stricklandinia, may be cited as examples. They cannot properly be correlated with similar parts in the ventral valve, for their origin is quite different. Primarily, a deltidial opening is for the extrusion of the pedicle and this belongs properly to the ventral valve. The dorsal fissure is the space between the diverging teeth sockets, and may be filled by the cardinal process, as in Leptæna and Orthis, or it may have in addition a convex plate or chilidium covering it, as in Clitambonites. In Spirifer and Stricklandinia, the opening remains unclosed.

The true deltidial plates are formed on the side of the pedicle adjacent to the hinge by extensions of the ventral mantle lobe, and begin as two plates. They are likewise expressive of maturity, and are of secondary development, while the deltidium begins as a single plate in the median line, and is eminently a primitive character in the Protremata.

From present knowledge of the group, it is difficult to offer an explanation for the presence of an anal opening in the Inarticulata and its absence in the recent Articulata, as the solution of the question depends upon whether the class is to be considered as progressive or degraded. The dorsal beaks of Amphigenia, Athyris, Cleiothyris, Atrypa, and Rhynchonella, are usually notched or perforate. The perforation comes from the union of the crural plates above the floor of the beak leaving a passage through to the apex. A similar opening occurs between the cardinal processes in Strophomena, Stropheodonta, and allied genera, and the chilidium may also be furrowed, as in *Leptæna* (=*Strophomena*) *rhomboidalis*. This character is evidently in no way connected with the pedicle opening, but points to the existence, in the early articulate genera, of an anal opening dorsal to the axial line, as in the recent Crania. This dorsal foramen was described and figured by King[13] in 1850, Hall[8] in 1860 and by several authors since, and has commonly been termed a visceral foramen.

Œhlert[21] suggests that it was probably occupied by the terminal portion of the intestine. The persistence of the foramen seems to indicate an anal opening. In reference to this character and the obsolescence of the eyes the class must be viewed as retrogressive since paleozoic time. Other features, however, are manifestly progressive; namely, the gradual shortening, through time, of the posterior elements of the animal, as the pedicle, visceral portions, and internal shell structures, and the expansion of the anterior parts, as the shell and brachia.

A further advance in specialization is shown in the limitation of the pedicle opening wholly to the ventral valve in the higher rhynchonelloids, athyroids, spiriferoids, and terebratuloids. The absence of punctæ in all the early radicles and their subsequent development in the derived types may also have a similar bearing.

The features and importance of the protegulum have previously been discussed.[1] It is merely noticed here as the embryonic shell of the completed phylembryonic period, for it is the first stage which can be observed among the fossil species, and is the initial point for the discussions of the relations and affinities of recent and fossil forms. Of the protegulum and later stages, there is abundant material available in nearly every family of brachiopods, ranging through their entire geological history.

Post-embryonic stages.

In discussing the post-embryonic stages of growth two aspects of development must be clearly differentiated; (*a*) the ontogenetical, and (*b*) the phylogenetical. The ontogeny of a form like Schizocrania may be conveniently divided into the nepionic, nealogic, and ephebolic periods, and such stages may be clearly defined. The ephebolic stage of Schizocrania, however, is like a nealogic stage of Orbiculoidea. In other words, Orbiculoidea, in its development, passes through a Schizocrania-like stage before reaching maturity.* These facts must be viewed from a phylogenetic standpoint. Moreover, in the geological history of a group, certain ephebolic characters of early species may become accelerated, and pass into the nealogic period of later forms, while other characters remain ephebolic. Discinisca offers an illustration of this. Its nealogic characters agree with Orbiculoidea in the form of the valves and in the pedicle notch, but the circular or elliptical form of the dorsal valve in adult and nealogic Orbiculoidea appears so early in Discinisca, that it marks all the nepionic stages. The interpretation of these facts is, of course, very evident, and will be subsequently given in detail. Attention is here called to the statement, that while nepionic, nealogic, and ephebolic stages represent equal intervals in the life of each individual, they do not represent conditions of growth, or the possession of characters which always agree stage for stage in the species of one family or of different families.

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* Attention was called to this fact in a publication preliminary to vol. viii of the Palæontology of New York, pp. 131, 132, issued February, 1890. Also the development of the pedicle opening in Orbiculoidea was fully described.

Other distinctions to be made whenever possible are (*a*) whether certain characters (natural or acquired) belong to a species by inheritance, or (*b*) are mere adaptations to special conditions of environment arising at any time in its history. A clear understanding of the first will lead to the true phylogeny of a species or genus, but to reach this the characters of the second category must be excluded. Thus in the series of Schizocrania, Orbiculoidea, and Discinisca, already cited, there is an apparent genetic connection in the facts as stated. The contrary must be the case with a shell like *Lingula complanata* Williams, and *L. riciniformis* Hall which initiate a holoperipheral[*] mode of growth in the ephebolic period, for this agreement in the method of concrescence with adult Orbiculoidea here appears in the mature stages of this species, and being absent in the early members of the genus cannot therefore be an ancestral character. It is a morphological equivalent, which may or may not be continued in the later species of the series.

Whenever features are present which can be referred to an ancestral origin, their elimination can take place only by the process of acceleration of development. On the other hand, there may be secondary characters of dynamical or homoplastic origin which appear simultaneously or independently in different groups belonging to diverse genetic lines, as the deltidial plates of the Rhynchonellidæ, Terebratulidæ, and Spiriferidæ. Further, many such secondary features may occur anywhere in the geological history of the group, as the high hinge area of Orthisina, Spirifer, Syringothyris, and Thecidium. These statements are in full accord with what Hyatt has determined in the Cephalopoda, and the application of such ideas affords a fertile field of research.

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[*] *ὅλὸς*, whole; *περιφε̃ρεια*, circumference.

Preliminary to a study of the stages of growth observed in the different orders, a simple characteristic example of each will be taken to show the limitations of the post-embryonic periods.

Nepionic period.—In brachiopods, as in pelecypods, this period represents the growth of the true shell immediately succeeding the embryonic shell or protegulum, and before the appearance of definite specific characters. In general, the nepionic shells of all groups are marked only by fine concentric lines of growth, and are therefore nearly smooth. Sometimes, however, a few radiating striæ or other ornaments may appear over the nepionic portion, but this is not the prevailing rule. *Obolus pulcher* Matthew shows a cancellated nepionic stage and is one of the most striking exceptional examples.

Plate I, figure 1, represents the nepionic stage of *Glottidia albida*, drawn from the beak of a well-preserved adult. The shell at this period had a short straight hinge (originally the hinge of the protegulum), with lines representing anterior and lateral growth, making the outline broadly ovate. It is divided from the succeeding growth of later stages by a strong varix. The form is suggestive of Obolella, and as this is the early form of growth of many of the Lingulidæ and allied families, it is here called the *Obolella-stage.* It is not known that otherwise the characters agree with those of Obolella, but as it is characteristic as well as descriptive the name is used to designate this form of nepionic growth whenever present.

The nepionic stage of *Orbiculoidea minuta*, figure 4, shows a continuance of the straight hinged condition after the completion of the embryonic shell, with nearly equal incremental lines. As this agrees with the shell of Paterina it is called the *Paterina-stage.* The pedicle emerged freely between the cardinal margins of the valves. It will be shown that both this and the Obolella-stage are represented in the nepionic periods of many genera belonging to the Atremata. They may succeed each other in a single species or one alone may be present. In case both appear, the Paterina stage is always the first one to be developed.

The nepionic stage of *Leptæna* (=*Strophomena*) *rhomboidalis*, fig. 7, Pl. I, is represented by a shell without radii, having a comparatively large pedicle opening in the ventral valve and a large deltidium. The hinge is not well defined and the shell is discinoid in form. This term is not used to suggest any special affinities with true discinoid genera, as Orbiculoidea or Discinisca. The proper name for this stage is not yet apparent to the writer. The external characters as expressed by both valves are manifestly nearer to Kutorgina than to any telotremate genus. Until the early forms belonging to the articulate brachiopods, especially to the orthoid and strophomenoid groups, have been thoroughly studied, the interpretation of the nepionic *Leptæna rhomboidalis* may be uncertain. It should be noted, however, that the young of Chonetes, Productus, Stropheodonta, Orthothetes, Leptæna, Plectambonites, and Strophomena, all have little or no indication of a straight hinge line, and that the extension of this member takes place during later nealogic and ephebolic growth. This in itself is significant, but is more marked when taken with the growth stages shown by some species of Strophomena which have after the protegulum, a Paterina-like stage, with straight hinge in dorsal valve, succeeded by holoperipheral, discinoid, nepionic growth, and finally a renewal of a straight hinged condition. Thus it has an early straight hinged form, which is lost during the next stage of growth, and again appears, and is progressively elongated during nealogic and ephebolic growth.

The nepionic stages of *Terebratulina septentrionalis*, fig. 10, Pl. I, represent a decreasing extension of the cardinal line from the protegulum, an open delthyrium, the absence of radii, and the introduction of the shell punctæ. The crura at this stage, as shown by Morse, are short and stout, and the loop is undeveloped.

Nealogic period.—During the progress of this period all the features which reach their complete growth in the adult organism are introduced and progressively developed. Usually they appear in succession, and gradually assume mature conditions. Thus in many species with radiate plications or striæ, a few radii appear in early nealogic growth, and are added to until the full number is present. Species with deltidial plates develop them in this period. The early stages may offer many points for comparison with the adult, but later stages usually differ little except in size. Figures 2, 5, 8, 11, Plate I, represent a nealogic stage in each of the four species taken as examples. Others from the same species could be given, but these suffice to show that one or more characteristic adult features have made their appearance.

Ephebolic period.—The period of complete normal growth, or the maximum of individual perfection. This corresponds to the adult, or mature organism, and is so well understood that no further explanation is necessary. For the sake of completing the series, the ephebolic shells of the species given are represented in figures 3, 6, 9, 12, Plate I.

Geratologic period.—The variations due to old age may be numerous and complex. As shown by Clarke and the writer,[3] the valves generally become thickened, and, as a consequence, the margins are truncate or varicose, the vertical diameter of the shell is increased, the beaks involuted, and the margins of the valves often lose the ornamentation characteristic of the species. The deltidial plates or deltidium may be resorbed as well as the beaks of the valves. Usually the ephebolic characters disappear in inverse order to their introduction. This is called the *clinologic stage* of geratology by Hyatt. Thus in a normal adult brachiopod having a plicate shell and deltidial plates, which characters were introduced during the nealogic period, the expression of old age will be found in the absorption of the deltidial plates and in the obsolescence of the plications. Large specimens of *Terebratella transversa* Sow. often furnish examples of this clinologic stage.

The geratologic development of Bilobites[2] consists in the obsolescence, in *B. varicus* Con., of the bilobed form of the shell, thus reverting to an early nealogic condition equally characteristic of *B. bilobus* and *B. Verneuilianus.*

Another aspect of growth and decline is manifest when the size of individuals and the chronological history of groups are taken into consideration. Each genus and family began with small representatives, and rapidly developed the more radical varieties of structure. Then came the culmination and final reduction in size, with abundance of geratologous and pathologic forms. The oldest known shell with calcareous spires, Zygospira, is a comparatively minute form. Nearly all the types of the suborder to which this genus belongs (Helicopegmata) appear in the Upper Silurian. Species presenting the maximum size belong to the Devonian and Carboniferous. Before the extinction of the suborder in the Trias, the individuals are small, and such abnormal genera as Thecospira, Koninckina, and Amphiclina, abound. Productus begins with small species (Productella) in the Lower Devonian, and in the Carboniferous attains the largest dimensions of any known brachiopod (*P. giganteus*). During the Permian, the species have dwindled in size, and the geratologous Strophalosia and Aulosteges are the chief representatives.

The culmination of geratologous growth results in the reversion of the animal to its own nepionic period, and is called the *nostologic stage.* As this is an extreme condition, it can be found only in certain genera and species which have been developed by a process of accelerated geratologous heredity. If Gwynia* is accepted as a valid genus, it belongs to a pronounced nostologic type. The shell has a small internal plate on each side of the dorsal umbo, evidently the bases of crural

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*Some authors have been disposed to consider this form as the young of a species not yet determined. It has also been referred to *Macandrevia cranium*, *Cistella cistellula*, and *C. neapolitana.* This question cannot at present be determined, although some characters of the shell indicate a mature organism.

plates. King,[14] the author of the genus, states that the labial appendages are attached directly to the shell, and not to a loop, as in other genera of the family. Cistella may be taken as a representative of nostologic development among the terebratuloids. The species are smooth, or pauciplicate, and small; deltidial plates obsolescent, loop more or less undeveloped. In *C. neapolitana*, the lamellæ of the loop are nearly obsolete and are free only near the crura, while the anterior portions are confluent with the valve (Shipley). A slight progression of these reversions would naturally result in a degenerate form like Gwynia, which is without a calcareous loop; with no surface ornamentation; deltidial plates absent, punctæ few and large, all of which features are strictly nepionic. Besides Cistella and Gwynia, other loop-bearing genera present nostologic features of importance in a natural classification. These consist mainly in their small size; the absence of surface ornaments; the obsolescence of deltidial plates, and the loss of a complete loop supporting the arms. In the Terebratulidæ, Kraussina and Platydia may be mentioned as belonging to geratologous types with a nostologic tendency. Likewise, in other groups, Atretia in the Rhynchonellidæ, and Strophalosia and Aulosteges in the Productidæ, are examples of nostologic types.

Cistella and Gwynia among the genera of brachiopods, therefore, bear the same relation to the terebratuloids that Baculites among the cephalopods bears to the ammonoids.

Synopsis.

Protembryo.—Ovum and segmented stages before formation of blastula cavity.

Mesembryo.—Blastosphere.

Metembryo.—Gastrula.

Neoembryo.—Trochosphere and cephalula, with posteriorly directed mantle lobes, and bundles of setæ from body segment.

Typembryo.—Larva with mantle lobes folded anteriorly over head segment.

Phylembryo.—Brachiopod covered by protegulum, tentacles of arms developed, bundles of setæ dehisced, definition of stomach and œsophagus, direct transformation of larval muscles into those corresponding to muscles of adult animal.

Deltidium.—A single plate developed at an early period by the body and pedicle of animal posterior to dorsal hinge, and later ankylosed to ventral valve.

Deltidial plates.—A nealogic and adult feature produced by the extensions of the ventral mantle lobe into the delthyrium.

Brachiopoda.—Retrogressive in loss of anal opening and eyes, progressive in concentration of posterior elements, expansion of anterior elements, and limitation of pedicle opening to one valve.

Nepionic period.—Young shells before the appearance of distinctive specific characters.

Nealogic period.—Progressive development of the specific features which reach their complete growth in the adult.

Ephebolic period.—Normal adult condition.

Geratologic period.—Special manifestations of old age in ontogeny and in phylogeny.

Nostologic types.—Extremes of geratology represented by Cistella, Gwynia, and Atretia.

Yale Museum, New Haven, Conn., May 31, 1892.

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EXPLANATION OF PLATE.

Glottidia albida Hinds.

FIGURE 1.—Nepionic shell; Obolella stage. × 36.
FIGURE 2.—Nealogic stage; showing anterior growth producing Lingula-like form. × 16.
FIGURE 3.—Ephebolic stage. × $\frac{3}{2}$.

Orbiculoidea minuta Hall.

FIGURE 4.—Nepionic shell; Paterina stage. × 36.
FIGURE 5.—Nealogic stage; first holoperipheral growth. × 16.
FIGURE 6.—Ephebolic stage. × 10.

Leptæna rhomboidalis Wilck.

FIGURE 7.—Nepionic stages, with short hinge. × 36.
FIGURE 8.—Early nealogic stage, with radiating striæ. × 10.
FIGURE 9.—Ephebolic stage. × $\frac{2}{3}$.

Terebratulina septentrionalis Couth.

FIGURE 10.—Nepionic stage, with open delthyrium. × 26.
FIGURE 11.—Early nealogic stage, with radiating striae. × 16. (After Morse.)
FIGURE 12.—Ephebolic stage. × $\frac{2}{3}$. (After Davidson.)

ART. XX.—*On some Double Halides of Silver and the Alkali-metals;* by H. L. WELLS and H. L. WHEELER. *With their Crystallography;* by S. L. PENFIELD.

DURING a systematic search for well crystallized salts of the type $M'Hl \,.\, AgHl$,* which we were anxious to obtain on account of their probable isomorphism with the alkaline trihalides, three well defined compounds of another type, $2M'Hl \,.\, AgHl$, were obtained. Our experience indicates that these 2 : 1 salts are more easily prepared and crystallize better than the 1 : 1 compounds.

The bodies to be described are $2CsCl \,.\, AgCl$, $2RbI \,.\, AgI$ and $2KI \,.\, AgI$. Two of these are believed to be new salts; the other, $2KI \,.\, AgI$ has been described by Boullay.† We have not obtained a complete series of these compounds, for good crystals could not be made of the other members, and, under the circumstances, no products were analyzed except such as could be measured.

The compounds are interesting from the fact that they do not conform to Remsen's law concerning the composition of double halides,‡ for, contrary to this, they contain a number of alkali-metal atoms which is greater than the number of halogen atoms belonging to the silver. In his latest contribution to the

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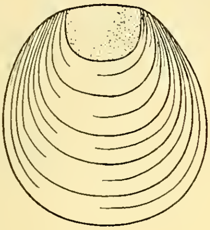
* This Journal, III, xliii, 30 and 485.
† Ann. Chim. Phys., II, xxiv, 377.
‡ Am. Chem. Jour., xi, 291.

Am. Jour. Sci., Vol. XLIV, 1892. Plate I.

Nepionic. Nealogic. Ephebolic.

1



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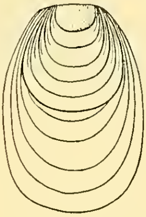

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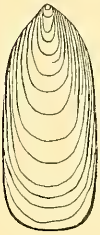

Atremata.

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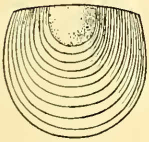

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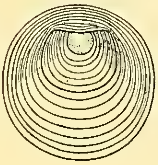

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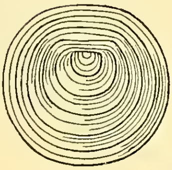

Neotremata.

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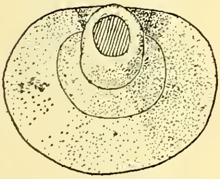

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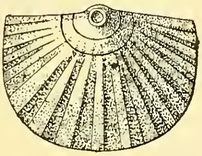

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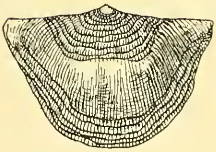

Protremata.

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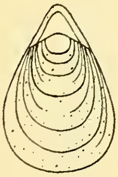

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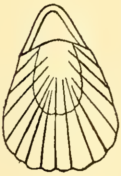

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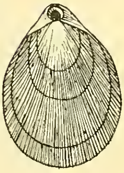

Telotremata.